

A preliminary report on the relationships of the indigobirds

by ROBERT B. PAYNE

Received 26th October, 1967

The African parasitic finches of the *Hypochera* group, the indigobirds or combassous, form a complex of variation which has proven to be unresolvable by the investigation of museum specimens alone. As each recent taxonomic review of the group has noted of its predecessors, the 14 described forms of indigobird consist of a hitherto unresolved number of species. The extremes of variation in the interpretation of species relationships of the birds suggest that all belong to a single, most variable species (White, 1963; Traylor, 1966 *sans* footnotes) or to as many as eight distinct species, some of them polytypic (Mackworth Praed and Grant, 1949). All the indigobirds (here considered to comprise the subgenus *Hypochera* of the genus *Vidua*) have male breeding plumage of black which is more or less iridescent with green, blue or purple. The females have generally been considered morphologically indistinguishable, although Mackworth-Praed and Grant (1949, 1960) and Roberts (1939) state without any explanatory remarks that females attributed to some forms differ from those of others. Some forms of indigobird have characteristic bill and foot colours. Taxonomic studies based on museum specimens have been limited by the failure of some collectors to note the bill and foot colour of specimens on the label at the time of collection. These colours change rapidly, within a day or two, after death and are not recognizable in museum specimens more than a few weeks after collection. Even more, taxonomic reviews of the indigobirds have not had available, until recently, any information on the biology of the living birds. Attempts to force the observed pattern of variation of the indigobirds into the concept of biological species have failed for this reason, and perhaps more significantly they have failed because these birds are better considered a group of cultural species.

I carried out extensive studies of the indigobirds in the field in five countries of Africa for two years (1966 and 1967). This field work is being continued and a comprehensive description of the field observations and a revision of the group are being prepared. Since this work will not be completed for some time, it seems advisable to present a preliminary statement on certain results of the field work in the possibility that it will lead other field workers to get the fullest information from their own studies. Future collecting of the indigobirds will be of little value unless the colours of the soft parts are noted at the time of collection. Future field work on the song of indigobirds and of their *Lagonosticta* song models will be of little use unless the singing birds are examined in the hand for species identification.

An operant description of the relationships of indigobirds has become possible largely because of the discovery by Nicolai (1964) that many viduines, including *Hypochera*, mimic the songs of their estrildine hosts. Nicolai found that each species of mimicking viduine sang the song of one and only one species of estrildine, in each case the known or suspected host species. He (Nicolai, 1967), D. N. Mansfield (MS cited in Traylor, 1966; also in personal communication) and I have heard all vocal mimicry of

the host song by these viduines in the field in Africa, thereby indicating that the mimicry reported by Nicolai of captive birds imported into Germany was not in fact a behavioural artifact of captivity. I have subsequently found during field observations of behaviour that mate selection by the female indigobirds is based on the host mimetic phrases of the song of the males. Since the mimicking viduines—both males and females—are apparently imprinted on the song of the host species by hearing the vocalizations of their foster parents and their host nestmates, the mechanism of behavioural isolation is one that is culturally transmitted by another species, not by their own parents. The extensive tape recordings which I made in the field and also the observations of behaviour and mate selection will be reported elsewhere. This brief description of the significance of host mimicry will permit the following discussion of the relationship of certain populations of the indigobirds.

Field studies were carried out using the following approach: singing males were tape-recorded, females mating with these birds were collected for specific identification and the recorded males were then collected and examined. The *Lagonosticta* species associated with each locality were observed and in several instances their songs were recorded and individuals were collected to verify the field identification. The relative abundance of the different forms of the indigobirds and of the firefinches were noted to provide evidence of the quantitative correlation of the geographical distributions of parasite and host. Because mate selection is based on the mimic song, forms of indigobirds which mimic the same species of host are themselves members of one traditional cultural species. This phenetic definition of cultural species is valid as a description of the genetic identity of populations regardless of the evolutionary history of each population. The results of the field study are briefly summarized in table 1.

The first important feature to note in table 1 is that three, not two, species of *Hypochera* occur in South Africa. The purplish-blue glossed, white-billed indigobirds of the Transvaal comprise two distinct species. One has red feet and mimics *L. rubricata* as does nominate *V. funerea* in Natal. As close as 30 miles from this population at Tzaneen, downstream from it along the Letaba River and in the more arid woodland of the Transvaal lowveld at Hans Merensky Nature Reserve, white-billed indigobirds have white feet and mimic *L. rhodopareia jamesoni*. White-footed males and red-footed males overlap completely in geographic range without any observed occurrence of birds with an intermediate pink or light orange foot colour. The overlap in range is readily apparent in the south-to-north alternation of white-footed birds and red-footed birds from Natal to Marble Hall to Tzaneen to Merensky to eastern Rhodesia. The morphological distinction between the two has been overlooked in the past (except by Roberts, 1939) because collectors in South Africa have generally neglected to note foot colour of specimens on the labels. As late as July, 1967, none of the 35 indigobirds in the collection of the Durban Museum had bill colour or foot colour recorded. The information about the one known morphologically differentiating character of the species is now permanently lost from such specimens.

The white-footed indigobirds of South Africa and of the remainder of Africa south and east of the Congo forests, as far as is now known, are best considered as members of the species *V. purpurascens*. The east

TABLE 1

Species relationships of the indigobirds of southern and eastern Africa

Locality	Described form	Song mimicked	Occurrence of <i>Lagonosticta</i>	Species of indigobird
South Africa				
Hluhluwe	<i>funerea</i>	<i>rubricata</i>	<i>rubricata</i>	<i>funerea</i>
Ndumu	<i>amauropteryx</i>	<i>senegala</i>	<i>senegala</i>	<i>chalybeata</i>
Marble Hall	* <i>amauropteryx</i> "funerea" (white feet)	<i>senegala</i> <i>rhodopareia</i>	<i>senegala</i> <i>rhodopareia</i>	<i>chalybeata</i> <i>purpurascens</i>
Tzaneen	* <i>funerea</i>	<i>rubricata</i>	<i>rubricata</i>	<i>funerea</i>
Merensky	**"funerea" (white feet) * <i>amauropteryx</i>	<i>rhodopareia</i> <i>senegala</i>	<i>rhodopareia</i> <i>senegala</i>	<i>purpurascens</i> <i>chalbeata</i>
Botswana				
Maun	*(<i>chalybeata</i>)	<i>senegala</i>	<i>senegala</i> <i>rhodopareia</i>	<i>chalybeata</i>
Rhodesia				
Lusitu	(<i>funerea</i>) "funerea" (white feet)	<i>rubricata</i> <i>rhodopareia</i>	<i>rubricata</i> <i>rhodopareia</i>	<i>funerea</i> <i>purpurascens</i>
Sabi Valley	* <i>amauropteryx</i> **"funerea" "white feet"	<i>senegala</i> <i>rhodopareia</i>	<i>senegala</i> <i>rhodopareia</i>	<i>chalybeata</i> <i>purpurascens</i>
Salisbury	"funerea" (white feet)	<i>rhodopareia</i>	<i>rhodopareia</i>	<i>purpurascens</i>
Atlantica	**"funerea" (white feet)	<i>rhodopareia</i>	<i>senegala</i> <i>rhodopareia</i>	<i>purpurascens</i>
Penhalonga	* <i>purpurascens</i> * <i>codringtoni</i> * <i>amauropteryx</i>	<i>rubricata</i> <i>senegala</i>	<i>rhodopareia</i> <i>rubricata</i> <i>senegala</i>	<i>purpurascens</i> <i>funerea</i> <i>chalybeata</i>
Malawi				
Chileka	<i>amauropteryx</i>	<i>senegala</i>	<i>senegala</i>	<i>chalybeata</i>
Zomba	* <i>codringtoni</i>	<i>rubricata</i>	<i>rubricata</i> <i>rhodopareia</i>	<i>funerea</i>
Monkey Bay	* <i>purpurascens</i> * <i>amauropteryx</i>	<i>rhodopareia</i> <i>senegala</i>	<i>rhodopareia</i> <i>senegala</i> <i>rhodopareia</i>	<i>purpurascens</i> <i>chalybeata</i>
Lilongwe	*(<i>purpurascens</i>) <i>amauropteryx</i>	<i>rhodopareia</i> <i>senegala</i>	<i>rhodopareia</i> <i>senegala</i>	<i>purpurascens</i> <i>chalybeata</i>
Lilongwe Airport	*(<i>purpurascens</i>) <i>amauropteryx</i>	<i>rhodopareia</i> <i>senegala</i>	<i>rhodopareia</i> <i>senegala</i>	<i>purpurascens</i> <i>chalybeata</i>
Salima				
Kenya				
Malindi	*(<i>amauropteryx</i>)	<i>senegala</i>	<i>senegala</i>	<i>chalybeata</i>
Nairobi	* <i>centralis</i>	<i>senegala</i>	<i>senegala</i> <i>rubricata</i>	<i>chalybeata</i>
Ologesailie	* <i>centralis</i>	<i>senegala</i>	<i>senegala</i>	<i>chalybeata</i>
Kisumu	* <i>centralis</i>	<i>senegala</i>	<i>senegala</i>	<i>chalybeata</i>
Sigor	*(<i>purpurascens</i>) * <i>centralis</i>	<i>rhodopareia</i> <i>senegala</i>	<i>rhodopareia</i> <i>senegala</i>	<i>purpurascens</i> <i>chalybeata</i>

* Asterisk indicates tape recordings of singing indigobirds.

African nominate *purpurascens* has a geographical distribution which corresponds *L. rh. jamesoni* in general. On the other hand the earlier name *nigerrima* has been applied in the past to the white-footed indigobirds of

Zambia and Malawi. However, toptypical *nigerrima* from north-western Angola—on historical grounds the probable type locality—corresponds in distribution not with *L. rhodopareia* but with *L. landanae*. Furthermore, these north-western Angola indigobirds have red, not white, feet. The names *purpurascens* and *nigerrima* thus appear to refer to different species.

The form *codringtoni* occurs in eastern Rhodesia as well as in Malawi and Zambia. Six adult males, five of them green and one more blue than green, were taken at Penhalonga in eastern Rhodesia. Each of the males mimicked the song of *L. rubricata*. *Codringtoni* is therefore a form of *Vidua funerea*. These green birds intergrade through an intermediate blue population along the lower Lusitu River in eastern Rhodesia with the purplish-blue nominate *V. f. funerea* of South Africa. The occurrence of *codringtoni* in Rhodesia (previously not known) was discovered as the result of a test of the "three species concept" of the indigobirds. It appeared probable that three species of indigobirds lived in Rhodesia if there were indeed three species in South Africa because the same three species of *Lagonosticta* (*L. senegala*, *L. rhodopareia*, *L. rubricata*) are common to these areas. In South Africa the red-footed *V. f. funerea*, mimics of *L. rubricata*, are geographically restricted to the moist habitats of the eastern Cape Province and northward and eastward along the continental escarpment, the range and habitat of this species of firefinch. In Rhodesia *L. rubricata* is restricted to the moist eastern border of the county (Benson and Irwin, in press). It was predicted that in areas of eastern Rhodesia a white-billed, red-footed indigobird would occur and would mimic the song of *L. rubricata*. The prediction was verified at Penhalonga and at the Lusitu River with the finding of *codringtoni* and the population intermediate between this form and nominate *V. funerea*.

Codringtoni has been considered by Traylor (1966) and by Nicolai (1967) to be a form of *Vidua chalybeata*. Traylor's consideration was based on the conception of the indigobirds as forming two species in southern Africa. He noted that the white-billed forms in Malawi and eastern Zambia were of two distinctly different kinds, one with red feet (*codringtoni*) and one with white feet. The plumage of these forms differed also within this circumspect area. Having apparently only two species available for the designation of aberrant forms, *V. chalybeata* was regarded as the more probable close relative of *codringtoni*. However, throughout the geographical range of *codringtoni* occurs another race of *V. chalybeata*: *V. c. amauropteryx*. This red-billed form mimics the song of *L. senegala*, (see table 1). More direct evidence for the parasitism than mimicry alone of *L. senegala* by *V. c. amauropteryx* is available for southern Africa, and Morel (1962) has made extensive observations of the parasitism of *L. senegala* by *V. c. chalybeata* in west Africa. Clearly two subspecies of the same species cannot by definition have the same geographical ranges. Thus *codringtoni* cannot be a subspecies of *V. chalybeata* in the exact same localities where *V. c. amauropteryx* occurs. The field observations and tape recordings of *codringtoni* as well as the finding of populations with the same song intergrading with *V. f. funerea* clearly establish *codringtoni* as specifically distinct from *V. chalybeata*, and as conspecific with *V. funerea*.

Nevertheless, Nicolai (1967) has just reported that *codringtoni* in Tanzania mimics the song of *Lagonosticta senegala*. His reports of mimicry, like the claims of the present preliminary report, are not documented by

sonograms of the songs. There can be little doubt from his earlier work with *L. senegala* (Nicolai, 1964) that he did record an indigobird mimicking this firefinch. However, museum specimens indicate that in central Tanzania two distinct populations of greenish to bluish, white-billed, red-footed indigobirds occur, both *V. f. codringtoni* and also *V. chalybeata* populations sharing characters of the southern race *amauropteryx* and the race to the north, *centralis*. Inasmuch as none of the reported "*codringtoni*" were apparently collected after their songs were recorded, it is not possible to know which form of the cryptic sibling species of indigobirds were actually recorded.

Similarly, the identification by Nicolai (1967) of the mimicry of the song of *L. rubricata* by the form of indigobird he called *purpurascens* is open to question. In this instance I question the identification of the firefinch. Both *L. rubricata* and *L. rhodopareia* have trilled phases in their songs. No distinction is made between these songs but rather a distinction is made between trilled songs in the species in question and the absence of varied phrases in *L. senegala*. From the photograph of the rather dry habitat where the tape recordings were made (Nicolai, 1967: fig. 1), it seems likely that the local species of trilling firefinch is *L. rhodopareia*, not the more mesophyllic *L. rubricata*. Collection of the local forms of firefinch or publication of the differences in song of the firefinches and the indigobirds would permit this question to be resolved.

It is here suggested that the form *purpurascens* is a distinct species. The sample of males recorded and collected in eastern Rhodesia and in Malawi included several purple birds with white feet and white bills. These agree in morphological characters with *purpurascens* from Tanzania in museum collections. All of these birds recorded in the field mimicked the song of *L. rhodopareia jamesoni*. A system of relationships based on the mimic song includes the white-footed, less glossy birds of southern Africa in *V. purpurascens*.

Collectors, please record the bill and foot colour. Recorders, please identify the birds by collecting them and comparing them with properly identified museum specimens.

For their helpful suggestions in the course of the study I am grateful to D. M. Eccles, M. P. S. Irwin, M. A. Traylor, C. M. N. White, J. A. Williams and J. M. Winterbottom. Field work was supported by a research fellowship from the National Science Foundation.

References:

- Mackworth-Præd, C. W., and Grant, C. H. B., (1949). On the indigo-birds of Africa. *Ibis*, 91, 98-102.
- (1960). Birds of eastern and north-eastern Africa. *African Handbook of Birds*, ser. 1, vol. 2. Longmans, London.
- Morel, G., (1959), Le parasitisme de *Lagonosticta senegala* (L.) par *Hypochera chalybeata* (Muller). *Ostrich*, suppl. 3, 157-159.
- Nicolai, J., (1964). Der Brutparasismus der Viduinae als ethologisches Problem. *Zeitschr. f. Tierpsych.*, 21 (2), 129-204.
- (1967). Rassen- und Artbildung in der Viduinengattung *Hypochera*. 1. *Hypochera funerea purpurascens* Reichenow- Brutparasit beim Dunkelroten Amaratent *Lagonosticta rubricata* (Lichtenstein). *Jour. f. Ornith.*, 108, 309-319.
- Roberts, A., (1939). *The Birds of South Africa*. H. F. and G. Witherby, London.
- Traylor, M. A., (1966). Relationships in the combassous (sub-gen *Hypochera*). *Ostrich*, suppl. 6, 57-74.
- White, C. M. N., (1963). The Indigobirds. *Bull. Brit. Orn. Club*, 83, 83-88.